

Comparison of Diaphyseal Growth Between the Libben Population and the Hamann-Todd Chimpanzee Sample

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ABSTRACT The differences in limb lengths and proportions between humans and chimpanzees are widely known. Humans have relatively shorter forelimbs and longer hind limbs than chimpanzees. Humans have a longer period of long bone formation than chimpanzees.

Recent advances in estimating age-at-death in chimpanzees from their dentition have allowed us to reexamine long bone growth in chimpanzees using their skeletal remains and compare it with similar data for humans. A chronological normalization procedure allowing direct interspecific comparison of long bone growth is presented. The preadult chimpanzee sample ($n = 43$) is from the Hamann-Todd Osteological Collection from the Cleveland Museum of Natural History. All human specimens ($n = 202$) are from the late Woodland Libben Population currently housed at Kent State University.

Relying on these cross-sectional data, we conclude that both species elongate their femora at similar absolute (length per unit time) but different relative (length relative to normalized dental age) rates. The species differ in the absolute growth rate of the humerus but share a common normalized rate of growth. Forelimb segment proportion differences between species are due to differential elongation rates of the segments. Hind limb diaphyseal proportions are the same in both species, which suggests that changes in segment length are proportional. Therefore, alternative developmental mechanisms exist in these closely related species which can produce changes in limb length. © 1996 Wiley-Liss, Inc.

Explanations of morphological differences between taxa are of two general types: ultimate (functional) and proximate (developmental/genetic). The relative limb proportions of modern chimpanzees and humans differ significantly (Schultz, 1926, 1936, 1940, 1956; Gavan, 1953). Such differences are clearly related to locomotor pattern: knuckle-walking and the complex climbing repertoire of the former, and habitual bipedality in the latter. The "ultimate" causation of these differences lies in their mechanical and functional effects on locomotion.

Of equal concern is their "proximate cause" (the ontogenetic mechanisms by which they emerge). For example, what developmental factors have been modified to produce their characteristic limb proportions? If normalized for differences in body size in the two taxa, are changes in length largely restricted to one limb or the other,

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or do they involve significant differences in both?

Chimpanzees have an absolutely shorter period of long bone growth than humans, yet their forelimbs are approximately the same absolute length. What developmental factors can be modified to produce morphological novelty? Are the absolute length differences and proportions between chimpanzees and humans a consequence of the very different developmental duration or are other local or systemic ontogenetic factors producing the species-specific differences?

Previous research on long bone growth in the chimpanzee has been presented by Schultz (1926, 1930, 1936, 1937, 1940, 1956) and Gavan (1953, 1971; Watts and Gavan, 1982). Schultz's extensive reviews of great ape growth, in which he relied on cross-sectional and longitudinal data of both soft and hard tissue growth, built the foundation for all subsequent studies of hominoid growth. He emphasized that interspecific comparisons must be based on normalized data. Schultz proposed that auxologic mosaicism (heterochrony) was the primary mechanism producing interspecific morphological variation in limb size, shape, and proportion in primates. He noted that limb proportions and rates of growth could change markedly between subsequent age intervals (Schultz, 1926, 1940) thus providing an ontogenetic mechanism of evolutionary change.

Gavan (1953) also conducted extensive research on chimpanzee growth. Unlike Schultz, he relied exclusively on longitudinal data of known-aged chimpanzees, thus overcoming the problems of using wild-shot specimens (i.e., unknown chronological age and uncertain living and health conditions). Like Schultz, Gavan clearly recognized the problem of comparing species of different size and applied a series of size normalization procedures. He observed that the absolutely longer chimpanzee ulna grows at a faster rate but for a shorter duration than its human counterpart. By contrast, humans show a faster growth rate for the thigh, leg, and upper arm when compared with trunk length. Absolute femur growth rate in both species was recorded by Gavan to be initially similar, with chimpanzees presenting a decreasing rate of elongation while humans

maintain this higher rate for a longer duration.

In subsequent research, Gavan and Swindler explored the absolute rate of sitting height growth in macaques, chimpanzees, and humans "to determine whether there is or is not evidence for a phylogenetic change in growth rate independent of the change in duration of time available for growth" (Gavan and Swindler, 1966, p. 181). Although agreeing with Schultz's observations on chimpanzee growth, Gavan and Swindler noted that his use of cross-sectional data of poorly aged specimens forced him to rely on indirect (i.e., skeletal) measures of absolute growth rate. Consequently, the "methods [used by Schultz] cannot distinguish among (1) change in rate per unit time, (2) constant rate but change in duration of time, and (3) change in both rate and duration of time" (1966, p. 182). These authors had clearly defined both the goals of comparative growth studies and the limitations of retrospective analyses.

Relying only on data from known-age specimens, Gavan and Swindler (1966) presented age-specific growth velocities of the trunk for the macaques, chimpanzees, and humans. They suggested that not only primates, but perhaps all larger mammals elongate their trunk at the same fundamental rate. Differences in trunk length among the anthropoids was then seen as a consequence of growth duration and not necessarily differences in rate. Unfortunately, Gavan and Swindler were unable to normalize for duration of growth between the species except to be aware of gross temporal differences.¹ As they recognized, differences in both size and growth duration confound interspecific comparisons.

In this paper, we elaborate on the previous descriptions of and comparisons between chimpanzee and human long bone growth. Although many of the points addressed here were raised previously (Schultz, 1926, 1937, 1940, 1956; Gavan, 1953, 1971; Gavan and

¹"Even though 2-year-old monkeys and chimpanzees or 8-year-old chimpanzees and children may be growing at the same average rate, they are certainly not at the same stage of physiological development. We have no answer to this problem" (Gavan and Swindler, 1966, p. 188).

Swindler, 1966; Watts and Gavan, 1982), we suggest that reanalysis of these data may yield new insight into the role of growth studies as a means of making interspecific comparisons. Despite the reservations raised by Gavan (1953; Gavan and Swindler, 1966) regarding the use of cross-sectional data, we suggest that the improved quality of assessing developmental age from dental remains, particularly in apes (Dean and Wood, 1981; Anemone et al., 1991) allows more fine-grained chronological studies to be conducted using existing skeletal collections. Cross-sectional analyses allow for a larger sample size (particularly of apes) than longitudinal studies. Ultimately, these data may prove helpful in reconstructing the history of adaptation of a species and perhaps outline developmental processes as a whole.

MATERIALS AND METHODS

All human specimens ($n = 202$) are from the Libben population, a ca. 1,000-year-old late Woodland cemetery collection from north-central Ohio (Lovejoy et al., 1977) which is curated by the Kent State University Department of Anthropology (Kent, Ohio). Maximum length of the diaphysis was measured for all preadult long bones. Specimens ranged in age from 6 months in utero to adult. Diaphyseal length of specimens with fused epiphyses was estimated. The chimpanzee sample ($n = 43$) was obtained from the Hamann-Todd collection (Cleveland Museum of Natural History, Cleveland, Ohio). Maximum diaphyseal lengths were collected using standard osteometric procedures.

Long bone diaphyses were chosen for this study because they are a permanent record of growth. Given that diaphyseal morphology bears a strong relationship to both body size (Schultz, 1937; Jungers, 1982) and locomotor function (Robinson, 1972; Lovejoy and Heiple, 1970; Lovejoy, 1975), it can be a useful indicator of both growth and behavior.

Because Schultz (1937) noted that long bone length asymmetry in chimpanzees is limited (normally less than 1%), right and left sides were measured interchangeably. In humans, the right upper limb is generally longer than its antimere, whereas the magnitude of lower limb asymmetry is small

(Schultz, 1937). Because these differences are minor, both right and left side measurements were collected for this study.

The Libben and chimpanzee samples

The two samples have different collection histories. The Libben juvenile sample is composed of individuals that suffered an early death and may not represent an unbiased segment of the population from which they were drawn (Johnston, 1962). For example, there is an inverse relationship between age-at-death and tooth crown size (Guagliardo, 1982; Simpson et al., 1990a). Growth, morbidity, and mortality are not entirely unrelated. However, Lovejoy and coworkers (1990) demonstrated that the pattern of long bone growth in the Libben group is comparable to a healthy human sample.

The wild-shot chimpanzee sample from west Africa was collected independent of individual health status. Overall, the juvenile chimpanzee sample is probably healthier than the human group as it shows a much lower frequency of morbidity in the skeletal remains (e.g., periosteal reactions, caries, enamel hypoplasias or hypocalcifications) (pers. obs.).

Normalization of the growth period

Humans have an absolutely longer period of growth lasting (depending on the parameters analyzed and research cited) about one-and-a-half times to twice as long as the chimpanzee. Many ontogenetic phenomena could be used to normalize the duration of growth between the species, e.g., age of menarche or age of fusion of selected epiphyses. Human epiphyseal growth is approximately 1.2–1.6 times longer than in chimpanzees (Watts, 1985) and age of sexual maturity in human females is approximately 1.5–1.7 times longer than in female chimpanzees (Gavan and Swindler, 1966; Watts, 1985; Harvey et al., 1987).

Dental ontogeny was chosen because it has been shown to be highly correlated with other life history and developmental events (Hurme and VanWagenen, 1961; Gavan and Swindler, 1966; Smith, 1989) and because it is less susceptible to developmental disruption than other systems (Garn et al., 1965). Plus, it is a continuous process beginning prior to birth

and can continue beyond sexual maturity. Development of the permanent dentition in both species has been discussed extensively (Schultz, 1935; Moorrees et al., 1963; Nissen and Riesen, 1964; Dean and Wood, 1981; Anemone et al., 1991; Simpson et al., 1990b, 1991, 1992; Smith, 1991; Kuykendall et al., 1992). The duration of human dental development is approximately 1.8–1.9 (years between birth and third molar emergence [Schultz, 1936, 1940; Smith, 1986]) or 1.96 (postconception age of third molar emergence [Gavan and Swindler, 1966]) times as long as in chimpanzees. In addition, redundancy of age estimate is emphasized because each specimen's dental age is a summary value calculated from multiple teeth. Juvenile dentitions used in this study contribute to the normalizing function throughout the actual period of development. Therefore, the normalizing value is not simply a ratio of single or terminal events (e.g., menarche, epiphyseal fusion).

The age normalizing function used here was derived by calculating chimpanzee ($n = 49$) and human ($n = 81$) dental ages for each specimen using both chimpanzee and human dental developmental schedules (Fig. 1). The relationship between the two series of age estimates was then used as the normalization function. Data on the timing of chimpanzee dental development were derived from the work of Anemone and coworkers (1991). The human schedule used here was also from the work of Anemone and coworkers (1991), which is a variant of a schedule originally presented by Dean and Wood (1981) from data collected by Moorrees and associates (1963). Chimpanzee and human ages were calculated using only the P4, M1, M2, and M3 teeth because we previously demonstrated that humans and African apes share a common pattern of postcanine dental development differing only in the duration of dental development (Simpson et al., 1990b, 1991, 1992). Clearly, the resulting normalizing function is dependent on the schedules used. However, as long as the same dental developmental schedules are used to age each specimen throughout the analysis, the same internally consistent relationship will be observed.

A linear relationship between the timing of postcanine ontogeny between the two

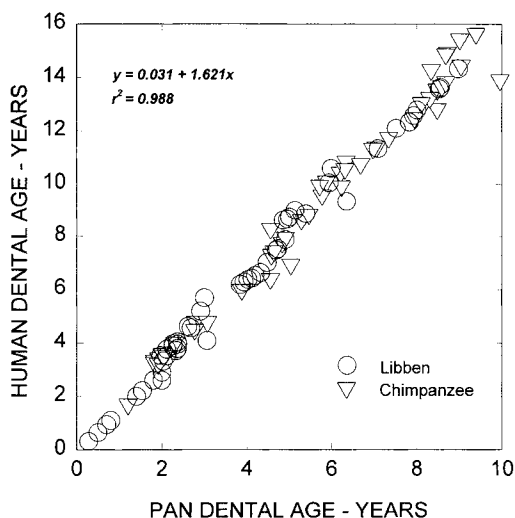


Fig. 1. Comparison of chimpanzee and human calculated ages (see text). Circles represent humans and triangles represent chimpanzees. Each specimen was assigned a summary chimpanzee and human dental age using the fourth premolar, and first, second, and third molars. Chimpanzee and human dental developmental schedules were derived from Anemone and coworkers (1991). The relationship between the two schedules is linear ($y = a + bx$; $a = 0.031$; $b = 1.621$; Pearson's $r = 0.994$; $r^2 = 0.988$).

schedules was observed (Fig. 1). Higher order functions did not significantly improve the quality of the model. Linearity of the relationship demonstrates the identity of developmental pattern in the postcanine dentition between the two species (Simpson, 1992). The y-intercept (0.03) does not differ significantly from zero. The slope (or interspecific ratio of dental age) of the function is 1.62, a fair compromise between those recently suggested by Smith (1.8 [1986]) and Bromage and Dean (1.5 [1985]). This correction factor improves upon those proposed previously because it is a cumulative and continuous comparison of dental development in both species applicable to each specimen throughout adolescence and not a simple ratio of single or terminal events.

RESULTS

Long bone lengths and proportions in adult chimpanzees and humans

Average adult total long bone lengths for chimpanzees and humans are listed in Table

TABLE 1. Average adult complete (diaphyses with fused epiphyses) long bone lengths (mm) for Libben and chimpanzee samples¹

	Libben	Pan	Libben/pan ($\times 100$)
Element			
Humerus	322.6	305.7	106
Ulna	277.1	294.3	94
Fore limb length (H + U)	599.7	600.0	100
Femur	445.0	297.1	150
Tibia	375.6	253.1	148
Lower limb length (F + T)	820.6	550.2	149
Ratio ($\times 100$)			
Humerus/ulna	116	104	
Femur/tibia	188	117	
Humerus/femur	73	103	
Fore limb/lower limb	73	109	

¹ Human adult means were calculated from samples of 51–77 male and 44–55 female complete adult left long bones from the Libben site. The chimpanzee adult means were derived from 10 male and 10 female adult chimpanzee long bones from the Hamann-Todd osteological collection. All measurements in millimeters.

1. Epiphyses contribute approximately 7–14% of the total adult long bone length (pers. obs.). In human and chimpanzee adult humeri with fused epiphyses, the humans have a somewhat longer mean length (about 5%). The ulnae shows a reversed pattern with the chimpanzees presenting a slightly longer (about 5%) element. Thus, when the two element's lengths are combined, the sums between the two species are indistinguishably different. The human lower limb (and each of the contributing bones) is about 50% longer in humans than chimpanzees.

Humerus length in preadult chimpanzees and humans

During the first 24 months, the human humerus rapidly increases in length (Fig. 2A). After this age, the rate slows until about 110 months. Following 110 months, the data become increasingly variable, due in part, perhaps, to sexual differences in ontogeny. Final diaphyseal length is attained between 180 and 240 months.

In the chimpanzee sample, the age range is attenuated with no cases younger than two years (Fig. 2A). Subsequent elongation appears to occur at a linear rate with full length achieved at about 120 months. The absolute rate of growth is faster than in similarly aged humans. Final length is achieved in the two species in absolutely different periods at absolutely different rates. Both the human and chimpanzee postinfancy growth rates appear linear.

When the duration of chimpanzee growth

is normalized (Fig. 2B; Table 2), the data overlap extensively. Chimpanzees have a similar *relative* rate (mm/relative time) of humerus length increase as humans. The absolutely longer human humerus may be a consequence of the adolescent growth spurt (Watts and Gavan, 1982; Bogin, 1988 and citations therein). Thus, when the developmental duration is normalized both species exhibit a similar pattern of humeral growth. The ulna in both species present a similar ontogenetic pattern as the humerus (Fig. 3A,B).

Upper limb length in preadult chimpanzees and humans

When the ontogeny of absolute humerus and ulna lengths relative to each other are examined for the two species (Fig. 4A), chimpanzees and humans both demonstrate a linear relationship with slightly different slopes (Table 2). This simply demonstrates that chimpanzees have relatively longer ulnae (higher brachial index) than humans and this difference manifests itself developmentally quite early (Schultz, 1926, 1936).

When growth of both bones is measured in terms of percent of adult length attained (specimen length/adult mean), both species show similar slopes (Fig. 4B; Table 2). Even though the elements have species-specific absolute rates of growth the fundamental proportional relationship between the two bones is retained. With a slope approximating one and a y-intercept of zero, this comparison also demonstrates that the relative

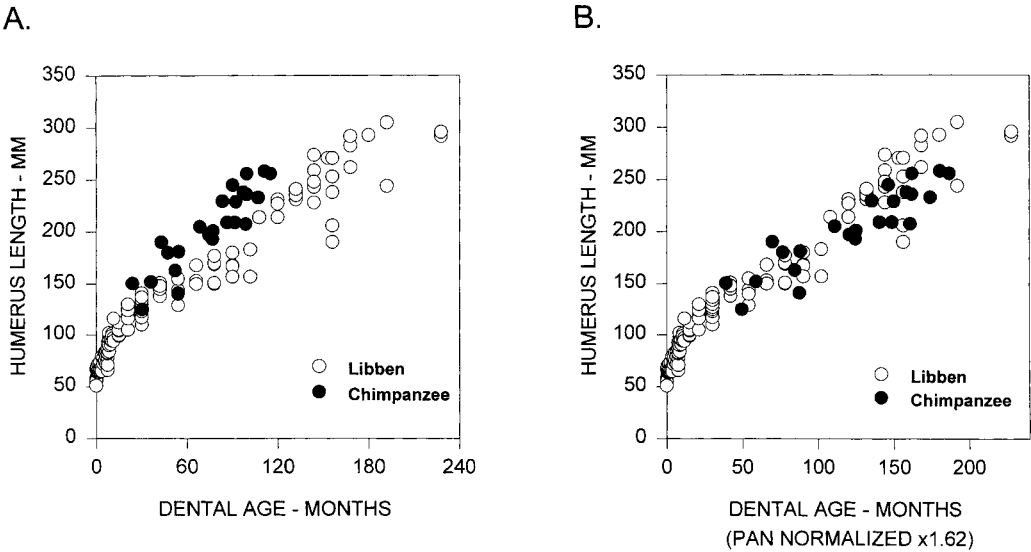


Fig. 2. Humeral diaphysis length in millimeters with dental age for chimpanzees and humans. Open circles represent humans and filled circles represent chimpanzees. Descriptive functions can be found in Table 2. **A:** Diaphysis length compared with absolute dental age. **B:** Diaphysis length with normalized dental age. Chimpanzee dental ages converted to human dental ages using function from Figure 1.

TABLE 2. Least squares regression summary for ontogenetic comparisons¹

	Libben			Pan		
	y-int	slope	r ²	y-int	slope	r ²
Humerus length with dental age	96.9	0.97*	0.915	106.1	1.29*	0.829
Humerus length with normalized age	96.9	0.97	0.915	106.1	0.80	0.829
Ulna length with dental age	86.2	0.81*	0.919	99.2	1.42*	0.899
Ulna length with normalized age	86.2	0.81	0.919	99.2	0.88	0.899
Ulna/humerus length	2.46	0.86*	0.996	6.32	0.98*	0.938
Ulna/humerus: % achieved	-0.02	1.06	0.968	0.02	1.01	0.938
Femur with dental age	123.6	1.42	0.941	96.0	1.40	0.885
Femur length with normalized age	123.6	1.42*	0.941	96.0	0.86*	0.885
Tibia length with dental age	105.1*	1.15	0.901	73.9*	1.22	0.882
Tibia length with normalized age	105.1*	1.15**	0.901	73.1*	0.75**	0.882
Tibia/femur length	-0.44	0.83	0.994	0.68	0.82	0.956
Tibia/femur: % achieved	-0.00	0.99	0.994	0.00	0.96	0.956

¹To make the age ranges comparable for the Libben and chimpanzee samples, all Libben specimens less than 20 months were omitted from the comparison. Each sample comparison was analyzed with an ANCOVA model (Snedecor and Cochran, 1967). For example, in order to compare human and chimpanzee samples for humeral growth with age, the following model would be used: $\text{Humerus length} = \beta_0 + \beta_1(\text{dental age}) + \beta_2(\text{taxon}) + \beta_3(\text{interaction})$ where "taxon" is the dichotomous variable (0 = Libben; 1 = chimpanzee) and "interaction" is the product of "dental age" and "taxon." β_3 is the difference in the slopes (rate of humerus growth) between the two groups and β_2 is the difference in y-intercepts. Unless indicated, Libben and chimpanzee samples are not statistically different (* $P < 0.05$; ** $P < 0.01$).

onset and cessation of elongation, duration, and relative rate of growth of the elements for the two species is the same. Not unexpectedly, the growth of the humerus and ulna are linked to some intrinsic developmental system in both species. As above, chimpanzees and humans adhere to differ-

ent absolute schedules yet maintain the same relative developmental schedule.

Femur length in preadult chimpanzees and humans

Humans and chimpanzees differ in both duration of femoral growth and final length.

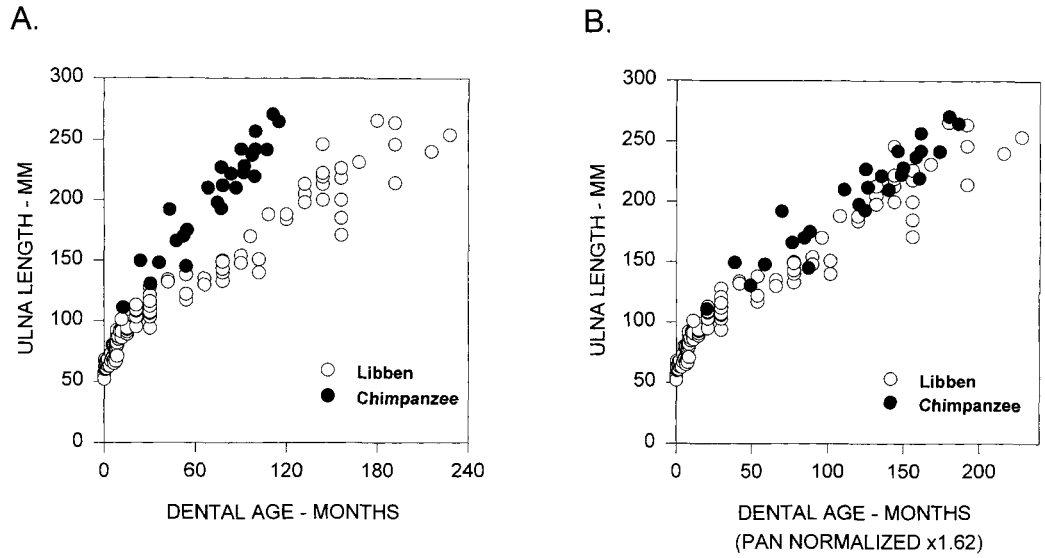


Fig. 3. Ulnar diaphysis length in millimeters with dental age for chimpanzees and humans. Open circles represent humans and filled circles represent chimpanzees. Descriptive functions can be found in Table 2. **A:** Diaphysis length compared with absolute dental age. **B:** Diaphysis length with normalized dental age. Chimpanzee dental ages converted to human dental ages using function from Figure 1.

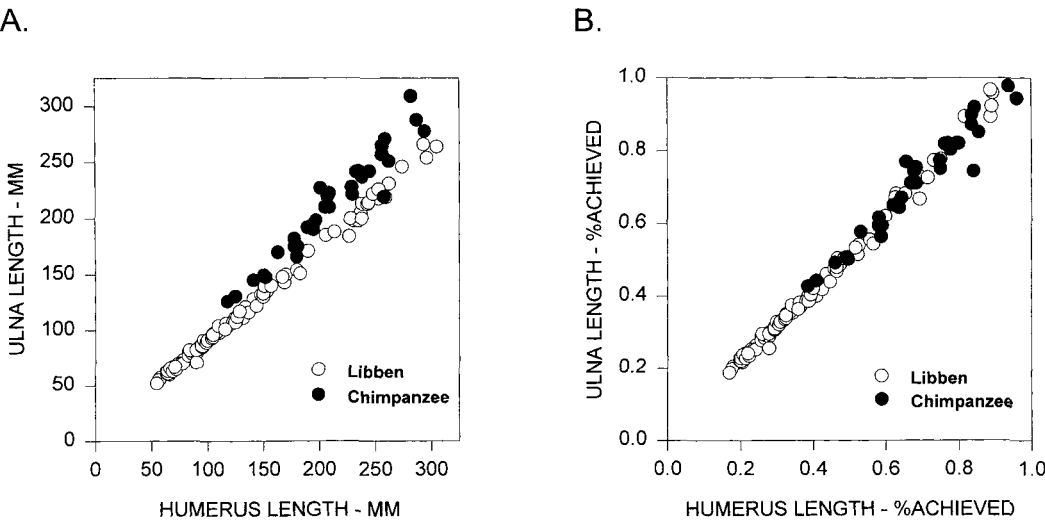
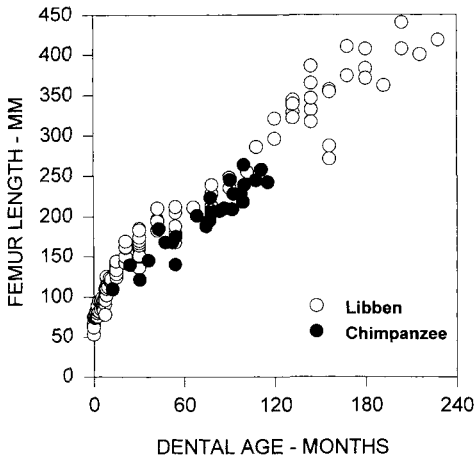


Fig. 4. Comparison of absolute and normalized ulnar and humeral diaphysis lengths for chimpanzees and humans. Open circles represent humans and filled circles represent chimpanzees. Descriptive functions can be found in Table 2. **A:** Absolute ulnar length with absolute humeral length. **B:** Normalized ulnar length compared with normalized humeral length. Each juvenile diaphysis length was divided by the appropriate adult sample

mean length (Table 1). Note that the largest specimens in both samples are approximately 90–95% of achieved length. Given that maximal length includes the epiphyses, whereas measured length only includes the diaphysis, unit would never be achieved. Epiphyseal proportions account for approximately 7–14% of the maximal length of the adult long bones. Therefore, maximal length is attained in both the humerus and the ulna.

A.



B.

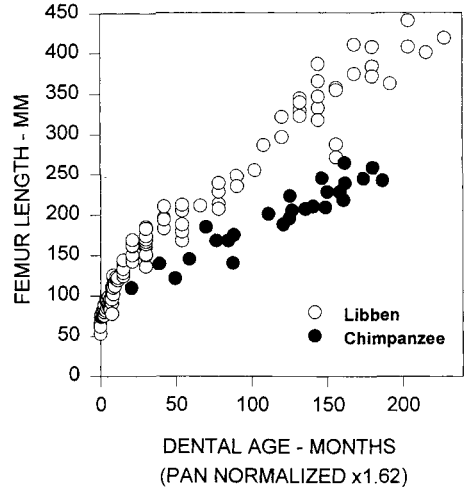


Fig. 5. Femoral diaphysis length in millimeters with dental age for chimpanzees and humans. Open circles represent humans and filled circles represent chimpanzees. Descriptive functions can be found in Table 2. **A:** Diaphysis length compared with absolute dental age. **B:** Diaphysis length with normalized dental age. Chimpanzee dental ages converted to human dental ages using function from Figure 1.

Both chimpanzees and humans older than 24 months show a roughly linear increase in femur length with time (Fig. 5A). The youngest humans present a decelerating curve between birth and 30 months. Femur elongation rate in both species is virtually identical beyond the age of 30 months.

When femoral length is compared with normalized age (Fig. 5B), chimpanzees show a significantly slower rate of normalized growth. Thus, differences in femur length are a consequence of either slowed growth (shortening) of the chimpanzee femur or a positive acceleration in human femoral growth rate. The pattern of tibial ontogeny (Fig. 6A,B) is similar to that of the femur.

Lower limb length in preadult chimpanzees and humans

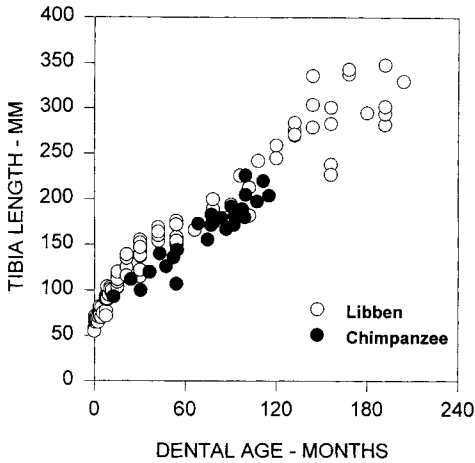
Unlike the upper limb, both species show a similar linear pattern of elongation of the tibia and femur throughout ontogeny (Fig. 7A,B). The constant ratios may reflect a common developmental relationship between these elements. This relationship holds for both absolute elongation (Fig. 7A) and percent attained (Fig. 7B) lengths. A similar

pattern was identified by Schultz (1940) for chimpanzees and gorillas but not monkeys.

DISCUSSION

Humans and chimpanzees have absolutely different growth schedules. Their upper limbs are approximately the same length yet humans have much longer lower limbs. How do these closely related species attain their characteristic lengths and proportions? Are all differences in long bone length simply a consequence of differences in developmental duration? Gavan and Swindler (1966) suggested that chimpanzees are larger than macaques because the chimps and monkeys grow at the same absolute rate but that chimps maintain this velocity over a longer period. These data show that chimpanzees have an absolutely faster rate of humeral elongation than humans. When these data are adjusted to match a common dental age, human and chimpanzee humeri present a very similar ontogenetic pattern. When seen in this light, chimpanzees do not have especially long humeri. They do however, have relatively and absolutely longer

A.



B.

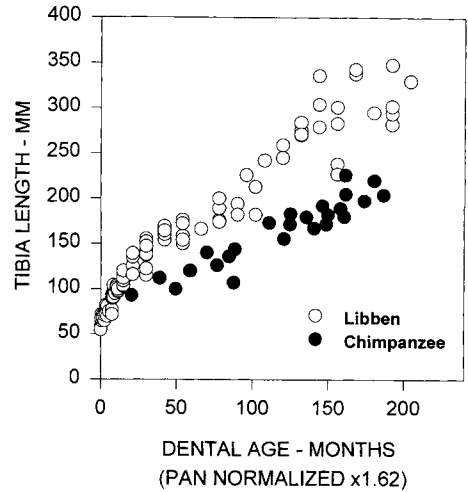
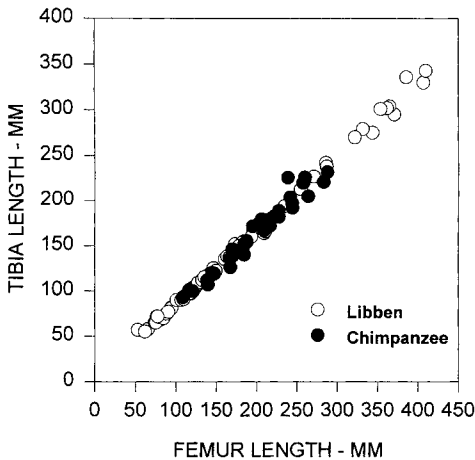


Fig. 6. Tibial diaphysis length in millimeters with dental age for chimpanzees and humans. Open circles represent humans and filled circles represent chimpanzees. Descriptive functions can be found in Table 2. **A:** Diaphysis length compared with absolute dental age. **B:** Diaphysis length with normalized dental age. Chimpanzee dental ages converted to human dental ages using function from Figure 1.

A.



B.

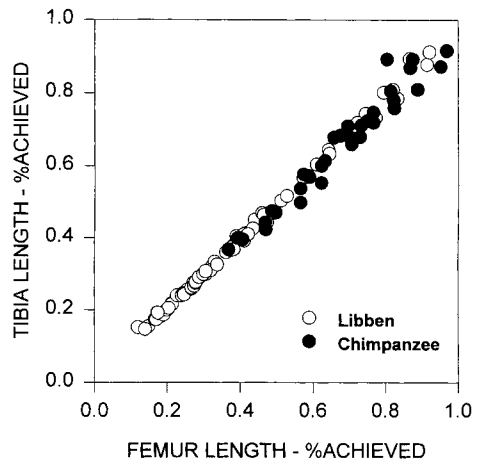


Fig. 7. Comparison of absolute and normalized tibial and femoral diaphysis lengths for chimpanzees and humans. Open circles represent humans and filled circles represent chimpanzees. Descriptive functions can be found in Table 2. **A:** Absolute tibial length with absolute femoral length. **B:** Normalized tibial length compared with normalized femoral length. Each juvenile diaphysis length was divided by the appropriate adult sample

mean length (Table 1). Note that the largest specimens in both samples are approximately 90–95% of achieved length. Given that maximal length includes the epiphyses whereas measured length only includes the diaphysis, unity would never be achieved. Epiphyseal proportions account for approximately 7–14% of the maximal length of the adult long bones. Therefore, maximal length is attained in both the tibia and the femur.

ulnae. The relative rate of growth between these elements in chimpanzees is approximately isometric. At any given age, the chimpanzee humerus and ulna are growing at the same proportional rate (% change in ulnar length/% change in humeral length). Humans, with their shorter ulnae, attain this length by elongating it at a slower relative rate than the humerus. This suggests that humans may have short ulnae instead of chimpanzees having long ulnae (Schultz, 1936). However, to completely identify changes in ontogeny between closely related species, the primitive condition shared by both groups should be identified.

When the ontogeny of the lower limb in chimpanzees and humans is examined, a different picture emerges. Apparently, both species share a similar absolute rate of femoral (and tibial) elongation. This observation could suggest that humans have long lower limbs only because of an extended period of development. Once this temporal normalization is performed, chimpanzees clearly show a slower rate of femoral growth resulting in their shorter lower limbs. This does not mean, however, that hominid femora have not elongated (Schultz, 1926, 1956; Jungers, 1982). It is possible and perhaps likely that both species have diverged from the ancestral condition. Again, knowledge of the ancestral condition is critical before this problem can be resolved. Finally, the ontogenetic relationship between the femur and tibia is the same in both species suggesting that despite changes in absolute length, they retain the primitive scaling ratio.

These data suggest multiple pathways to alterations in limb length dictated by the selective environment and ontogenetic variation. Either portions of the limb can change (as in the upper limb) or the entire limb can be proportionately modified (lower limb). The plasticity demonstrated in limb development is important to consider when making interspecific or historical comparisons.

Differences in growth rate between species is apparent ontogenetically early. Schultz (1926, 1936, 1940, 1956) noted that chimpanzee and human limb proportions varied throughout fetal and postembryonic development. Although no single value could consistently define the relationship (i.e., bra-

chial index or intermembral index) throughout development, chimpanzees and humans presented different limb proportions quite early (4–6 months in utero). Similarly, this was also noted by Jungers and Fleagle (1980) in their study of growth of the morphologically distinct, yet congeneric *Cebus albifrons* and *C. apella*. Even their youngest specimens presented characteristic differences in limb proportions.

But what are the proximate mechanisms which can produce gross morphological differences in closely related species (Alberch et al., 1979; Gould, 1977; Raff and Wray, 1989)? Both genetic and environmental factors have been identified which can alter long bone growth (Moss-Salentijn, 1992). Environmental mechanisms are useful for explaining variation of long bone length within populations, but genetically determined differences in growth are necessary to explain interspecific variation. These differences are produced by some alteration in the growth parameters of the physal plate cells. Changes in developmental duration are unlikely because both species initiate and terminate diaphyseal growth at approximately the same relative age (Figs. 4B and 7B, Table 2) showing an intercept of zero and a slope of one. Delaying the relative onset or termination of growth or changing the relative duration of growth of one of the elements would change either the y-intercept or the slope. Therefore, common systemic factors control the timing of onset and cessation of diaphyseal elongation in these species.

SUMMARY

Ideally, somatic measurements at known intervals can yield absolute measures of growth rate (Gavan, 1953; Gavan and Swindler, 1966), but absolute rate of change may not be a useful comparison in organisms with absolutely different developmental schedules. Therefore, some means of chronological normalization is necessary (Gavan and Swindler, 1966; Reiss, 1989; Lovejoy et al., 1990). In this paper, we presented a method by which species with different developmental durations can be directly compared. We then undertook a preliminary analysis

of diaphyseal ontogeny in chimpanzees and humans to explore possible mechanisms contributing to their characteristically different size and proportion.

Based upon measures of diaphyseal length in humans and chimpanzees, we observed the following. The upper limb bones in chimpanzees lengthen at an absolutely faster rate than humans. When elongation is normalized for developmental age, humans and chimpanzees exhibit a similar pattern of humeral diaphyseal growth. The humeri in both species share a common normalized developmental rate. Chimpanzees, however, have absolutely and relatively longer ulnae than humans and this difference manifests itself ontogenetically early. Chimpanzees achieve their long forelimbs (relative to humans) (Schultz, 1936) by lengthening the more distal segments. Differences in limb length are not simply a consequence of differences in developmental duration. Absolute growth rates of the femur and tibia are similar for both chimpanzees and humans. When normalized for ontogenetic duration, human femora and tibiae elongate at a faster normalized rate than those of chimpanzees. Despite their different rates of growth, both species maintain their long bone proportions throughout ontogeny. Therefore, the mechanisms by which chimpanzees achieve their relatively long arms and humans their long legs are different, being a consequence of both local and regional phenomena.

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LITERATURE CITED

- Alberch P, Gould SJ, Oster GF and Wake DB (1979) Size and shape in ontogeny and phylogeny. *Paleobiology* 5:296–317.
- Anemone RL, Watts ES and Swindler DR (1991) Dental development of known-age chimpanzees, *Pan troglodytes* (Primates, Pongidae). *Am. J. Phys. Anthropol.* 86:229–242.
- Bogin B (1988) *Patterns of Human Growth*. Cambridge University Press; Cambridge.
- Bromage TG and Dean MC (1985) Re-evaluation of the age at death of immature fossil hominids. *Nature* 317:525–527.
- Dean MC and Wood BA (1981) Developing pongid dentition and its use for ageing individual crania in comparative cross-sectional growth studies. *Folia Primatol.* 36:111–127.
- Garn SM, Lewis AB, and Kerewsky S (1965) Genetic, nutritional, and maturational correlates of dental development. *J. Dent. Res.* 44:228–242.
- Gavan JA (1953) Growth and development of the chimpanzee: A longitudinal and comparative study. *Hum. Biol.* 25:93–143.
- Gavan JA (1971) Longitudinal postnatal growth in the chimpanzee. In G Bourne (ed.): *The Chimpanzee*, Vol. 4. Basel: Karger, pp. 46–102.
- Gavan JA and Swindler DR (1966) Growth rates and phylogeny in primates. *Am. J. Phys. Anthropol.* 24:181–190.
- Gould SO (1977) *Ontogeny and Phylogeny*. Cambridge, MA: Belknap Press.
- Guagliardo MF (1982) Tooth crown size differences between age groups: A possible indicator of stress in skeletal samples. *Am. J. Phys. Anthropol.* 58:383–389.
- Harvey PH, Martin RD, and Clutton-Brock TH (1987) Life histories in comparative perspective. In BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham, TT Struhsaker (eds.): *Primate Societies*. Chicago, IL: University of Chicago Press, pp. 181–196.
- Hurme VO and Van Wagenen G (1961) Basic data on the emergence of permanent teeth in the rhesus monkey (*Macaca mulatta*). *Proc. Am. Philos. Soc.* 105:105–140.
- Johnston FE (1962) Growth of the long bones of infants and young children at Indian Knoll. *Am. J. Phys. Anthropol.* 20:249–254.
- Jungers WL (1982) Lucy's limbs: skeletal allometry and locomotion in *Australopithecus afarensis*. *Nature* 297:676–678.
- Jungers WL and Fleagle JG (1980) Postnatal growth allometry of the extremities in *Cebus albifrons* and *Cebus apella*: A longitudinal and comparative study. *Am. J. Phys. Anthropol.* 53:471–478.
- Kuykendall KL, Mahoney CJ and Conroy GC (1992) Probit and survival analysis of tooth emergence ages in a mixed-longitudinal sample of chimpanzees (*Pan troglodytes*). *Am. J. Phys. Anthropol.* 89:379–400.
- Lovejoy CO (1975) Biomechanical perspectives on the lower limb of early hominids. In RH Tuttle (ed.): *Primate Functional Morphology and Evolution*. The Hague: Mouton, pp. 291–326.
- Lovejoy, CO and Heiple KG (1970) A reconstruction of the femur of *Australopithecus africanus*. *Am. J. Phys. Anthropol.* 32:33–40.
- Lovejoy CO, Meindl RS, Pryzbeck TR, Barton TS, Heiple KG, and Kotting D (1977) The paleodemography of the Libben site. *Science* 198:291–293.
- Lovejoy CO, Russel KF, and Harrison ML (1990) Long bone growth velocity in the Libben population. *Am. J. Hum. Biol.* 2:533–541.
- Moorrees CFA, Fanning EA, and Hung Jr EE (1963) Age variation of formation stages for ten permanent teeth. *J. Dent. Res.* 42:1490–1502.

- Moss-Salentijn L (1992) Long bone growth. In BK Hall (ed): Bone. Vol. 6: Bone Growth A. Boca Raton: CRC Press, pp. 185–208.
- Nissen HW and Riesen AH (1964) The eruption of the permanent dentition in the chimpanzee. *Am. J. Phys. Anthropol.* 22:285–294.
- Raff RA and Wray GA (1989) Heterochrony: Developmental mechanisms and evolutionary results. *J. Evol. Biol.* 2:409–434.
- Reiss JO (1989) The meaning of developmental time: A metric for comparative embryology. *Am. Naturalist* 134:170–189.
- Robinson JT (1972) Early Hominid Posture and Locomotion. Chicago: The University of Chicago Press.
- Schultz AH (1926) Fetal growth of man and other primates. *Q. Rev. Biol.* 1(4):465–521.
- Schultz AH (1930) The skeleton of the trunk and limbs of higher primates. *Hum. Biol.* 3:303.
- Schultz AH (1935) The eruption and decay of the permanent teeth in primates. *Am. J. Phys. Anthropol.* 19:489–581.
- Schultz AH (1936) Characters common to higher primates and characters specific for man. *Q. Rev. Biol.* 11:259–283, 425–455.
- Schultz AH (1937) Proportions, variability and asymmetries of the long bones of the limbs and the clavicles in man and apes. *Hum. Biol.* 9(3):281–328.
- Schultz AH (1940) Growth and development of the chimpanzee. *Contrib. Embryol.* 170:1–63.
- Schultz AH (1956) Postembryonic age changes. *Primatologia* 1:887–964.
- Simpson SW (1992) Comparative Development of the Hominoid Dentition. Kent, Ohio: Ph.D. Diss., School of Biomedical Sciences, Kent State University.
- Simpson SW, Hutchinson DL, and Larsen CS (1990a) Coping with stress: Tooth size, dental defects, and age-at-death. *Anthropol. Papers Am. Museum Nat. History* 68:66–77.
- Simpson SW, Lovejoy CO, and Meindl RS (1990b) Hominoid dental maturation. *J. Hum. Evol.* 19:285–297.
- Simpson SW, Lovejoy CO, and Meindl RS (1991) Relative dental development in hominoids and its failure to predict somatic growth velocity. *Am. J. Phys. Anthropol.* 86:113–120.
- Simpson SW, Lovejoy CO, and Meindl RS (1992) Further evidence on relative dental maturation and somatic developmental rate in hominoids. *Am. J. Phys. Anthropol.* 87:29–38.
- Smith BH (1986) Dental development in *Australopithecus* and early *Homo*. *Nature* 323:327–330.
- Smith BH (1989) Growth and development and its significance for early hominid behavior. *Ossa* 14:63–96.
- Smith BH (1991) Standards of human tooth formation and dental health assessment. In M Kelley and CS Larsen (eds.): *Advances in Dental Anthropology*. New York: Wiley-Kiss, pp. 143–168.
- Snedecor GW and Cochran WG (1967) *Statistical Methods*, 6th ed. Ames, IA: Iowa State University Press.
- Watts ES and Gavan JA (1982) Postnatal growth of non-human primates: the problem of adolescent spurt. *Hum. Biol.* 54:53–70.
- Watts ES (1985) Adolescent growth and development of monkeys, apes, and humans. In ES Watts (ed.): *Nonhuman Primate Models for Human Growth and Development*. Philadelphia, PA: AR Liss, Inc., pp. 41–65.